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Structure and functioning of four North Atlantic ecosystems - A comparative study

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A B S T R A C T

The epi- and mesopelagic ecosystems of four sub-polar ocean basins, the Labrador, Irminger, Iceland and Norwegian seas, were surveyed during two legs from Bergen, Norway, to Nuuk, Greenland, and back to Bergen. The survey was conducted from 1 May to 14 June, and major results were published in five papers (Drinkwater et al., Naustvoll et al., Strand et al., Melle et al., this issue, and Klevjer et al., this issue a, this issue b). In the present paper, the structures of the ecosystem are reviewed, and aspects of the functioning of the ecosystems examined, focusing on a comparison of trophic relationships in the four basins. In many ways, the ecosystems are similar, which is not surprising since they are located at similar latitudes and share many hydrographic characteristics, like input of both warm and saline Atlantic water, as well as cold and less saline Arctic water. Literature review suggests that total annual primary production is intermediate in the eastern basins and peaks in the Labrador Sea, while the Irminger Sea is the most oligotrophic sea. This was not reflected in the measurements of different trophic levels taken during the cruise. The potential new production was estimated to be higher in the Irminger Sea than in the eastern basins, and while the biomass of mesozooplankton was similar across basins, the biomass of mesopelagic micronekton was about one order of magnitude higher in the western basins, and peaked in the Irminger Sea, where literature suggests annual primary production is at its lowest. The eastern basins hold huge stocks of pelagic planktivore fish stocks like herring, mackerel and blue whiting, none of which are abundant in the western seas. As both epipelagic nekton and mesopelagic micronekton primarily feed on the mesozooplankton, there is likely competitive interactions between the epipelagic and mesopelagic, but we're currently unable to explain the estimated ~1 order of magnitude difference in micronekton standing stock. The results obtained during the survey highlight that even if some aspects of pelagic ecosystems are well understood, we currently do not understand overall pelagic energy flow in the North Atlantic.

1. Introduction

The North Atlantic Ocean contains several major ocean basins including the Norwegian Sea, Iceland Sea, Irminger Sea, and Labrador Sea (Fig. 1). These four Arcto-boreal deep-water basins are adjacent, but despite their rather similar latitudinal position they have their own characteristics in terms of the bathymetry, hydrography, and ecology. The Norwegian Sea in the east harbours some of the largest populations of commercially exploited stocks as well as broadly distributed fish species (Skjoldal, 2004). The Iceland Sea is a feeding ground for pelagic fish including capelin, herring, and, in recent years, mackerel (Astthorsson et al., 2012; Huse et al., 2012). The western basins, the Labrador and Irminger seas, are inhabited by large populations of marine mammals and seabirds (Barrett et al., 2006). The Labrador Sea is also known for its high biomass of demersal shrimps while the Irminger Sea is considered a major site for carbon sequestration (Fröb et al., 2016).

The overarching objectives of the Euro-BASIN initiative were to investigate the population structure and dynamics of broadly distributed and biogeochemically and trophically important plankton and fish species of the North Atlantic basins and shelf seas. Further, we wanted to assess impacts of climate variability on North Atlantic marine ecosystems and their goods and services including feedbacks to the earth system, and to develop understanding and strategies that will contribute to improving and advancing management of North Atlantic marine ecosystems following an ecosystem approach.

The vicinity of the four high-latitude ecosystems, the Labrador, Irminger, Iceland, and Norwegian seas, makes it valuable to analyse the commonalities and differences in their forcing, structure and

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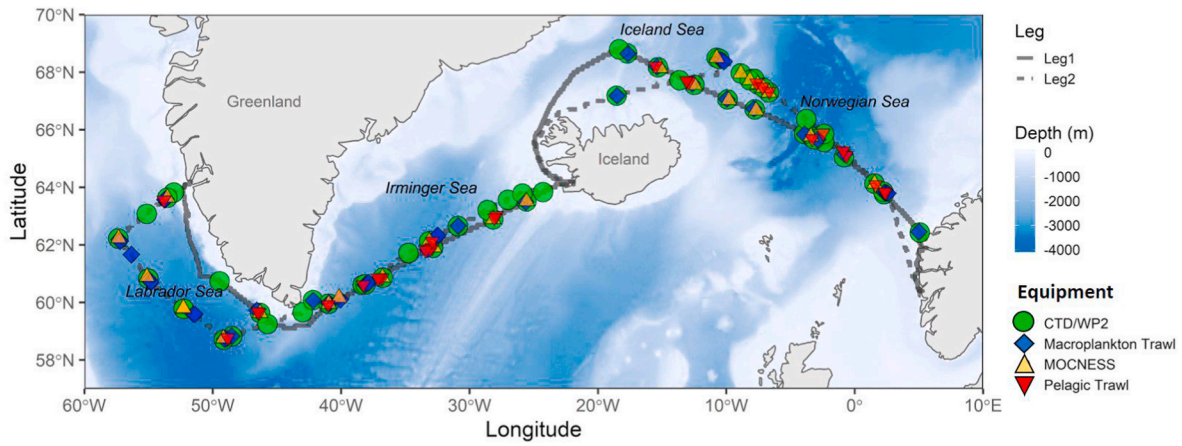

Fig. 1. Trans-Atlantic cruise with R/V G.O. Sars, 1 May to June 14, 2013. Cruise tracks with sampling stations.

functioning. These issues were addressed during a trans-Atlantic survey from 1 May to 14 June as part of the Euro-BASIN project funded during the EU 7FP. The sampling strategy included underway observations as well as sampling at key stations down to 1000 m with a variety of sampling gears and sensors that have been described in six previous studies (Drinkwater et al., Naustvoll et al., Strand et al., Melle et al., this issue, and Klevjer et al., 2020a). These studies report and compare characteristics at different sublevels of the four ecosystems, hydrography (Drinkwater et al., this issue), phytoplankton (Naustvoll et al. this issue), mesozooplankton and micronekton (Strand et al., Klevjer et al., 2020a), mesopelagic scattering layers (Klevjer et al., 2020b), and trophic interactions between zooplankton and herring (Melle et al., this issue). The present study synthesizes the main findings across trophic levels to reveal important commonalities and differences in structure and functioning of the four high-latitude ecosystems.

2. Basin characteristics

2.1. Physical structure

The physical oceanographic structure of the four basins was discussed in Drinkwater et al., (this issue). Each of the basins is influenced by warm, high salinity waters that are advected from the south and cold, low salinity waters originating from the north. The former water originates from the North Atlantic Current that crosses the North Atlantic from southwest to northeast while the latter water comes primarily from the Arctic via Fram Strait, although some Arctic Water to the Labrador Sea comes through Davis Strait. Differences between the basins arise from the amount of these waters that enter each basin and the mixing that occurs on route to, and within the basins, plus the addition of fresh water primarily from ice melt and glacial runoff, and local solar heating and cooling. The warmest surface waters in the four basins are typically found in the Norwegian Sea owing to the largest influence of North Atlantic Current waters. During the 2013 survey, surface waters in the Norwegian Sea were observed to have a maximum temperature of around 6 °C in early May at the beginning of the survey that rose to 10 °C by the time we returned in mid-June. This temperature increase was attributed mainly to solar heating. Surface salinities were as high as 35.2–35.3 with little change between the beginning and end of the survey. The Irminger Sea surface waters were slightly cooler than the Norwegian Sea but with nearly the same salinities. Sampling in the Irminger Sea was approximately 2 weeks later than in the Norwegian Sea during the westward phase of the survey and 2 weeks earlier during the eastward phase, which can explain some of the observed temperature difference.

The Iceland and Labrador seas were cooler and fresher than the Norwegian and Irminger seas due to the greater influence of the Arctic waters. These Arctic waters flow off the adjacent shelves and into the deep basins of these seas, stratifying the water column. Surface waters in the Iceland Sea were at a maximum of 2 °C during the westward transect but rose to 6 °C on the return trip. Again, this increase was attributed mainly to solar heating as salinities did not change being 34.7–34.9 on both legs. The central Labrador Sea was only surveyed on the eastward leg. At that time, surface temperatures were between 5-6 °C and salinities between 34.2-34.7.

All four basins were vertically stratified with a deep mixed layer early in the survey but became shallower in late spring. Deep winter convection in the Labrador and Irminger seas typically occurs each year, reaching down to 2000 m and beyond in some years (Våge et al., 2011; Yashayaev and Loder, 2016). During the 2013 survey, the mixed layer depths during the westward leg were between approximately 200-340 m but by late spring decreased to 124 m in the Irminger Sea and to 10–20 m in the Iceland and Norwegian seas. In the Labrador Sea, the mixed layer depth was estimated to be around 80 m. At the time of crossing, the bloom conditions in the Labrador Sea led to high levels of light attenuation, and therefore the estimates of euphotic zone depth (Klevjer et al., 2020b) were much smaller than the estimated mixed layer depth.

The largest difference in the hydrography of the four basins during the survey was in the temperature and density of the deep waters (depths >1000 m). While the Irminger and Labrador seas deep water temperatures and salinities were similar, they were warmer and hence less dense than the deep waters in the Norwegian and Iceland seas. The deep-water salinities were similar in all four basins with values around 34.91. The temperature difference between the two sets of basins is due to the larger and more direct influence of the cold waters from the Arctic.

The hydrographic anomalies in the Norwegian, Iceland, Irminger, and Labrador seas in the late spring of 2013 were slightly warmer and of higher salinity than the long-term means. However, they were within the historical variability of these regions.

2.2. Phytoplankton and nitrate structure

Naustvoll et al. (this issue) summarise observations of the phytoplankton communities and their dynamics in the four basins. The primary production dynamics of the four basins were compared and related to physical forcing and top-down control and discussed in relation to vertical carbon flux. The focus was on the primary production dynamics in the central, mostly Atlantic, water masses of the basin-wide gyres.

Phytoplankton bloom development, or phenology of the phytoplankton communities, differed among the four seas. In the Labrador Sea, there was a strong bloom at the time of the first survey of the seas, while in the other seas, and particularly the Irminger Sea, bloom development lagged. In the Norwegian and Iceland seas, the state of the

Table 1
Migration estimates: Estimates of components of vertical connectivity.

	Standing stock		Migrating proportion		Mesopelagic backscatter	Migrating backscatter	Migrator biomass	
	Total mesozooplankton biomass	Total fish biomass	OPC based	Acoustic based (38 kHz MP)	Daytime 38 kHz backscatter	Direct acoustic estimate 38 kHz	Mesozooplankton	Mesopelagic fish
LS	1.05	1.85	0.19	0.18	568	104	0.20	0.33
IRS	1.33	3.18	0.12	0.09	1292	112	0.16	0.29
ICS	1.79	0.06	0.11	0.09	65	6	0.19	0.01
NS	1.54	0.07	0.45	0.78	377	293	0.69	0.06
Unit	g C m^{-2} 0–200 m	g C m^{-2} 0–1000 m			m^2 nmi^{-2}	m^2 nmi^{-2}	g C m^{-2} d^{-1}	g C m^{-2} d^{-1}
Note	1	2	3	4	5	5	6	7

1: Data from Strand et al., this issue; WP2 nets 200-0 m, dry weights converted to carbon using conversion for general plankton from Wiebe (1988): Log(DW) = 0.508 + 0.977Log(C). 2: From Klevjer et al., 2020a, based on WW in trawl catches 1000-0 m, converted to carbon using conversion for general plankton from Wiebe (1988): Log (ww) = -1.597 + 0.852Log(C). 3: Data from Strand et al, this issue, based on diel changes in biovolume from OPC deployments. 4: Data from Klevjer et al., 2020b, based on loss of 38 kHz backscatter from mesopelagic depths during night. 5: Data from Klevjer et al., 2020b, Table 1. 6: Product of 1 and 3. 7: Product of 2 and 4, assuming that 100% of the 38-kHz backscatter originates from fish.

blooms changed from a pre-bloom to a late bloom situation from the first to the second crossing, while the bloom did not appear to have started in the Irminger Sea. In the Labrador, Iceland and Norwegian seas the use of nitrate was evident, with reduced amounts in the upper 100 m. While the bloom in the Irminger Sea was particularly late and its development slow, the high winter nutrient values and somewhat deeper spring and summer mixed layer suggests that new production in the Irminger Sea could exceed that of the Norwegian Sea by 100%. Across all basins an inverse relationship between the depth of the shallowing mixed layer and the use of nitrate suggests that bloom development and phenology of the phytoplankton are related to water column stabilisation. There was also a direct relationship between the use of nitrate and chlorophyll concentrations. Satellite data confirmed that the Norwegian and Irminger seas are characterised by low chlorophyll conditions during spring and summer, without pronounced chlorophyll accumulation. The Iceland Sea, and particularly the Labrador Sea, showed more intense blooms. The satellite data also confirmed that the bloom in the Labrador Sea commenced earlier than in the other seas. The early and strong bloom in the Labrador Sea has been related to early water column stabilisation by advection of low salinity surface waters from the West Greenland Shelf. At the time of the survey, there were no clear signs of nutrient limitation of the blooms in any of the four basins. Flagellates were the most numerically abundant algae in all regions, outnumbered by diatoms only in a couple of near-shelf stations west of Greenland. Elevated ciliate numbers were observed in the regions of the East Greenland Current, the shelf stations around Iceland, and during the eastward crossing in the Iceland and Norwegian seas on both sides of the Arctic front. The algae outnumbered the microzooplankton by at least an order of magnitude.

In the Labrador Sea, the presence of chlorophyll fluorescence at mesopelagic depth was a direct indication of vertical loss of biomass and carbon from the mixed layer during the vigorous bloom taking place. The potential for carbon vertical transport in the Irminger Sea is probably high due to the high winter nutrient concentrations and, consequently, high new production, but the late and slow bloom may imply that more of this flux comes in the form of fecal pellets, if grazing within the mixed layer can match the primary production. The same may be the case for the Norwegian Sea.

2.3. Mesozooplankton structure

WP2 net catches (180 μm mesh, 0–200m) of mesozooplankton showed similar levels of total biomass in the different basins (Strand et al., this issue), with the only significant difference in the biomass levels being more biomass of larger forms (mainly *Calanus hyperboreus* and cheatognaths) in the Iceland Sea. In the Iceland Sea, small (180–1000 μm), medium (1000–2000 μm) and large (> 2000 μm) mesozooplankton fractions contributed equally to overall biomass. In the Irminger Sea, the 1000–2000 μm fraction was the largest contributor to overall biomass, whereas in both the Labrador and Norwegian Seas, the smallest fraction was dominant. Mesozooplankton was also sampled and analysed taxonomical with a 1 m^2 MOCNESS (180 μm mesh) on select stations with nets opening/closing at 0-25-50-100-200-400-600-800-1000 m depths. Across all basins, a total of 9 different species/groups were found to comprise the 5 most numerically important species/groups per basin, with *Oithona* spp. being the most common genus in all basins. *Calanus finmarchicus* was found to be the most numerically common species of the *Calanus* spp. in all basins, but the stage composition varied markedly between basins, with young copepodite stages dominating only in the Labrador and central Norwegian seas. The vertical distribution of mesozooplankton in terms of abundance, measured as weighted mean depth (WMD), was shallower in the Norwegian seas compared to the other basins. Numerically, chaetognaths, *Metrida* spp., *Oncaea* spp. and *Pseudocalanus* spp. were on average found in higher densities in the two eastern basins compared to the western ones (Strand et al., this issue). *Paraeuchaeta* spp., on the other hand, was more numerous in the Irminger Sea compared to the Iceland and Norwegian seas. Although the Iceland and Labrador seas had significantly more chaetognath biomass (0–200) than the Norwegian Sea, in terms of numerical abundance within the same depth range, the Norwegian had almost the same integrated densities as the Iceland sea and more than 3x that of the Labrador Sea which indicate a much larger individual size of chaetognaths found e higher in the Labrador and Irminger seas than in the Iceland Sea.

2.4. Macroplankton and micronekton structure

For the macroplankton and micronekton components, the trawl catches showed large differences between the western and eastern basins, with the western basins having both higher overall biomasses and higher diversity in the catches (Klevjer et al., 2020a). Whereas biomass densities of crustacean components were similar between the basins, both scyphozoan and teleost densities were at least one order of magnitude higher in the Irminger and Labrador seas (Klevjer et al., 2020a, see also Table 1).The hull-mounted acoustics suggested that epipelagic nekton was only present in the eastern basins (e.g. Iceland and Norwegian seas), with no fish schools detected in the epipelagic zone in the western basins during the cruise (Klevjer et al., 2020a).

Most of the micronektonic biomass was acoustically assigned to the mesopelagic zone during daytime, and the hull mounted acoustics documented pronounced deep scattering layers (DSLs) in the mesopelagic zone in all basins (Klevjer et al., 2020b). In terms of depth, the centre of gravity of the vertical distributions varied from ~305 m (WMD) in the Labrador Sea to ~500 m in the Irminger Sea. Variations in

Table 2
Estimates of standing stock biomasses or production levels for different components investigated during the survey. "Macroplankton" is used to cover both macroplankton and micronekton, to the extent that there is any distinction between the two. Notes:

	LS	IRS	ICS	NS	Unit	Note
New production	59 (1)	36 (2)	70(3)	39-40 (1)	g C m^{-2} yr^{-1}	N1
Total annual primary production	144 (1)	35-45 (4)	80 (3)	80 (1)	g C m^{-2} yr^{-1}	N1
MLD @ Cruise	80	124	20	20	m	N2
Summer MLD	10(5)	21(6)	30(7)	25(8)	m	N1
Nitrate @ 200 m	14.1	13.7	12.3	11.7	μM	N3
Direct estimate NP	13	26	22	21	g C m^{-2} yr^{-1}	N4
ZPB [0–200m] < 1000 μm	0.62	0.54	0.65	0.88	g C m^{-2}	N5
ZPB [0–200m] 1000–2000 μm	0.26	0.70	0.56	0.57	g C m^{-2}	N5
ZPB [0–200m] >2000 μm	0.16	0.08	0.56	0.08	g C m^{-2}	N5
Crustacean macroplankton	0.66	0.77	0.63	0.28	g C m^{-2}	N6
Teleost macroplankton	1.85	3.18	0.06	0.07	g C m^{-2}	N6
Cnidarian macroplankton	0.32	0.41	0.04	0.02	g C m^{-2}	N7
Epipelagic nekton	Absent	Absent (N5)	Seasonal	Seasonal (N5)	Present/absent	N8

N1: Values from literature: 1: Harrison et al. (2013). 2: Sanders et al. (2005). 3: Skogen et al. (2007). 4: Waniek and Holliday, 2006. 5: Harrison and Li (2007). 6: Holliday et al. (2006). 7: Palsson et al. (2012). 8: Rey (2004).
N2: Data from Drinkwater et al., this issue, MLD during the last crossing of the basin.
N3: Data from Naustvoll et al., this issue.
N4: New production estimated from nitrate values at 200 m depth, and summer MLD's from literature, assuming 100 % consumption of nitrate down to a depth of the summer MLD, and 0 outside, and a Redfield ratio of C:N 163:22.
N5: Data from Strand et al., this issue; Zooplankton biomass from WP2 nets 200-0 m, dry weights converted to carbon using conversion for general plankton from Wiebe (1988): Log(DW) = 0.499 + 0.991Log(C).
N6: From Klevjer et al., 2020b), based on WW in trawl catches 1000-0 m, converted to carbon using conversion for general plankton from Wiebe1988: Log(ww) = -1.597 + 0.852Log(C).
N7: Data from Klevjer et al. (2020a), based on WW in trawl catches 1000-0 m, converted to carbon using conversion for *Periphylla periphylla* from Kiørboe, 2013).
N8: Both *Sebastes* in IRS and blue whiting in NS are here considered as mesopelagic species, alternatively these are 2 nektonic species that have a more permanent presence in these basins.

light attenuation could explain most of this variability, and the centre of gravity of the scattering was found close to a common light level across all basins (Klevjer et al., 2020b). The data also documented pronounced differences in migration patterns across the basins. In the Norwegian Sea, most of the backscatter from the DSL migrated from mesopelagic depths to the epipelagic during night; similar patterns were seen in the Iceland Sea, but there the scattering layers never reached the epipelagic, but stopped their migrations at mesopelagic depths (Norheim et al., 2016). In both western basins, diel vertical migration (DVM) from the DSL's was detectable, but only a lower fraction of the backscatter participated, with the majority of backscatter remaining close to daytime depths during night (Table 1).

The combination of acoustic and trawl data suggest that the migrating biomass is higher in the western basins (Table 1). The proportion and absolute level of migrating backscatter between the epi- and mesopelagic is largest in the Norwegian Sea (Klevjer et al., 2020b), however the levels of total mesopelagic backscatter are ~2–4 times higher in the Labrador and Irminger Seas than in the Norwegian Sea, and the trawl catches had ~15 to ~25 times higher biomasses of mesopelagic fish in the west (Klevjer et al., 2020a). A common assumption is that backscatter at 38 kHz is dominated by organisms with gas-inclusion (Irigoien et al., 2014), which in the areas explored by us would be predominantly fish (Klevjer et al., 2020a). With a fish biomass ranging from 0.06 to 3.61(g C m^{-2} 0–1000 m; Table 1) and a migrating proportion based on 38 kHz backscatter ranging from (0.09–0.78), the migrating mesopelagic fish biomass would be 3–4 times higher in the western basins compared to the two eastern basins (Table 1). Alternatively, if one assumes that the acoustic properties of the vertically migrating fish are similar across the areas, i.e. that one unit backscatter correspond to one unit biomass across all basins, the data would show higher migrating biomass in the Norwegian Sea. This would imply that less than 1% of the fish biomass in the Irminger Sea is involved in vertical migration (e.g. for methods and data see Klevjer et al., 2020b, especially their Table 1) and it becomes hard to conceptually balance the energy budgets of the mesopelagic ecosystems in the west, and one would have difficulties explaining the processes of energy flow into the mesopelagic depths in the western areas. In the following we assume that the migrating biomass observed on 38 kHz is totally dominated by fish, which also implies that the acoustic properties of the fish varied among areas.

2.5. Arctic Front planktivore structure

Melle et al. (this issue) observed the horizontal and vertical distribution of herring during their feeding migration on a very fine scale along a 128 km transect across the Arctic Front between the Norwegian and Iceland seas in early June. They found that the Arctic Front was an important transitional zone with pronounced changes in zooplankton biomass, abundance, and diversity. Phenology of phyto- and zooplankton also changed across the front, development being somewhat delayed on the cold side. The herring were distributed all along the transect showing a shallow distribution (0–50 m) on the warm side and both deep (100–250 m) and shallow distribution on the cold side, not clearly related to light and time of the day. The herring stomach content was higher on the cold side. There was no significant pattern in average age, weight, or body length of the herring along the transect. The herring were present and fed in the area of the transect during the time when the overwintering generation of *Calanus finmarchicus* dominated in surface waters, before the development of the new generation of the year. We suggest that the phenology of *C. finmarchicus* can be an important driver of the herring feeding migration. While prey-availability was higher on the Arctic side of the front, light conditions for visual feeding at depth were probably better on the Atlantic side. The herring did not show classical diel vertical migration, but its prey did, and the herring's prey (e.g. both meso- and macrozooplankton found in herring stomachs) were available within the upper 100 m during a 24 h cycle. With a general westward direction of migration, the herring along the transect moved towards lower temperatures, but the study of Melle et al. (this issue) suggests that improved feeding opportunities might be the underlying driver for the westward migration. Thus, more emphasis on fine-scale studies of herring migration and feeding are required to increase our understanding of herring large-scale migration and distributional patterns.

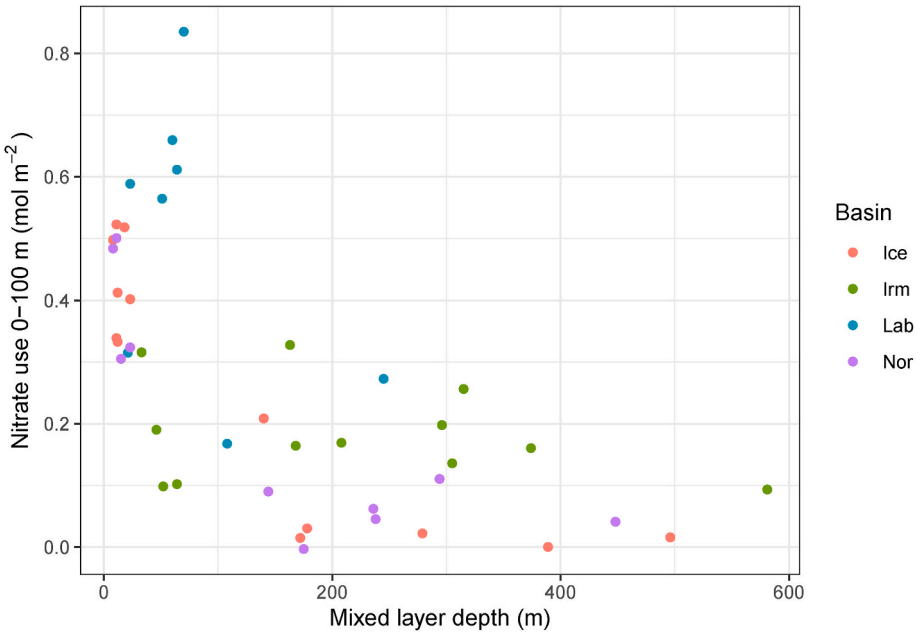

Fig. 2. Nitrate depletion versus mixed layer depth. After Naustvoll et al. (this issue).

3. Functioning of the ecosystems

3.1. The physics, nutrients, primary production, and higher trophic levels' biomass

Table 2 summarises basic characteristics of the physics, nitrate concentrations, and primary production of the four ecosystems. The first three rows summarise estimates of annual new and total primary production and estimates of summer MLDs from literature. The next two rows contain the MLDs and nitrate concentrations at 200 m as observed during the survey, while the 6th row shows estimated new production based on literature values for summer MLDs and measured nitrate concentrations at 200 m during the survey. The literature survey clearly indicates that the Labrador Sea is the most productive area, while at the other end of the spectrum, the Irminger Sea appears rather oligotrophic (Table 2). Summer MLDs vary between 21 and 30 m in the Irminger, Iceland and Norwegian seas, while in the Labrador Sea summer MLD ends up at only 10 m. During the survey, we observed MLD of 80–124 m in the western basins and only 20 m in the eastern basins. Nitrate concentrations at 200 m, indicative of winter values after the deep overturning event, were around 14 μM in the western basins and around 12 in the eastern basins, indicating a higher potential for new production in the west. If the summer MLD and nitrate at 200 m are used to calculate new production, as described in the footer of Table 2, the results are similar for all basins, except for the Labrador Sea where new production is only about half of the other seas. Surely, using summer MLD for this calculation is an oversimplification of the dynamic process of the MLD shallowing and phytoplankton production. At the time of the survey there was a strong bloom in the Labrador Sea already, while the MLD was observed at about 80 m (Table 2). This shows that nitrate far below

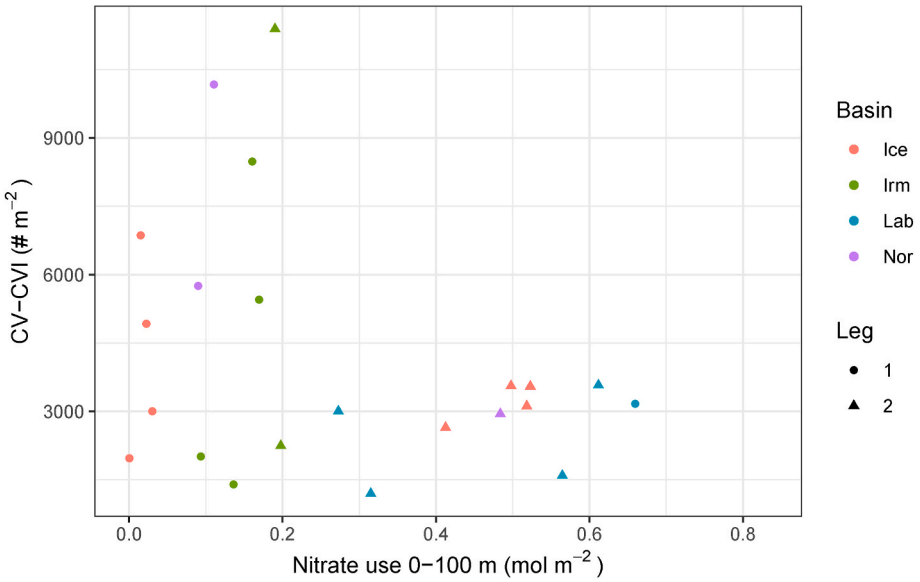

Fig. 3. Surface-integrated number of individuals of *Calanus finmarchicus* stages CV-CVI (# m^{-2}) from vertically integrated MOCNESS net samples (0–200 m) versus the depletion of nitrate (mol m^{-2}). After Strand et al. (this issue).

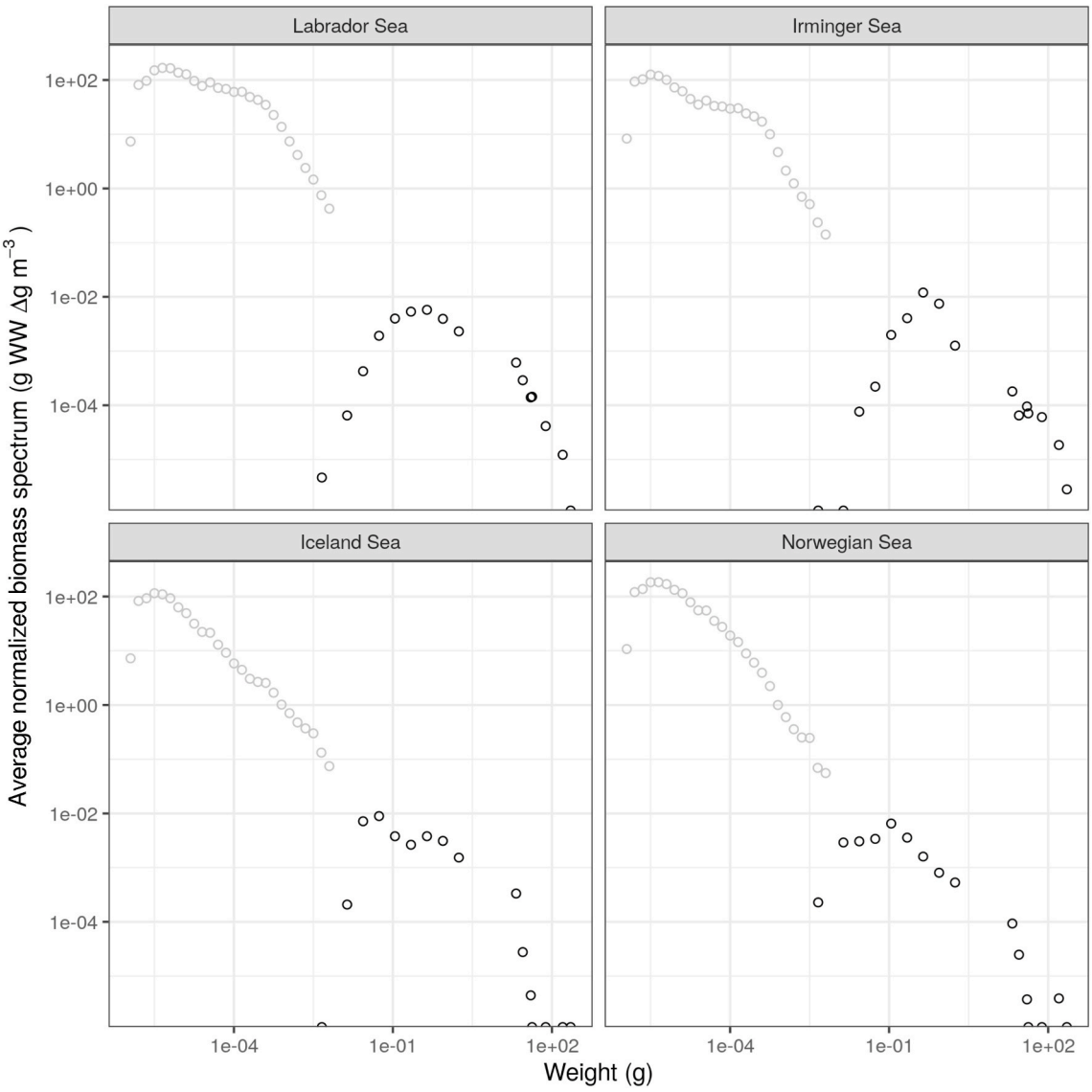

Fig. 4. Combined normalized biomass spectra from OPC counts and trawl catches. Grey circles show normalized biomass spectra (e.g. estimated density (wet weight) of particles per size class, divided by size class width) plotted against particle weight estimated from the OPC data (Strand et al., this issue). Black circles show the same measure from trawl catches (Klevjer et al., 2020a). Note that the decline in biovolume at smaller sizes in the trawl represent the mesh-size selectivity of the netting.

summer MLD will be available for the phytoplankton production and therefore modelled results or *in situ* measurements of spring-time production can yield higher values as shown in Table 2. Nevertheless, high nitrate concentrations after winter mixing in the two western seas are indicative of high potentials for new production, which only appears to be realised in the Labrador Sea (Naustvoll et al., this issue).

The rather oligotrophic appearance of the Irminger Sea is not mirrored either in the biomass of the mesozooplankton, macroplankton, micronekton nor the cnidarian plankton (Table 2). In all groups the biomass of higher trophic levels peaks in the Irminger Sea, only partly matched in the Labrador Sea. Table 2 does not give an estimate of epipelagic fish biomass present per unit surface in the eastern basins, however, based on the calculations in APPENDIX B the biomass per unit surface of herring, mackerel and blue whiting is 0.22, 0.08, 0.07 g C m^{-2}, within their observed distribution areas in the Norwegian and Iceland seas, and for mackerel, the northern Irminger Sea. Based on these back-of-the-envelope calculations of the pelagic fish stocks' biomass, they are major contributors to the predatory community of the eastern basins. However, if one takes the higher P/B ratio for the macroplankton and micronekton into account (Skjoldal, 2004), the contribution by pelagic fish to the total predatory consumption, is reduced. Nevertheless, the pelagic fish stock biomass is not high enough to explain the discrepancies between the western and eastern basins in the ratio between primary production and higher-level biomass (see discussion below). Rather there seems to be an underestimation of the primary production in the Irminger Sea or a higher trophic efficiency especially in this sea compared to the others. When comparing to the adjacent Labrador Sea, the slower development of the phytoplankton bloom may suggest enhanced transfer from primary to epi-pelagic secondary producers at the expense of passive flux (Naustvoll et al., this issue). However, this is a paradox that we cannot fully explain, but which is discussed in more detail below.

3.2. *Phenology; mechanisms and opportunities for higher trophic levels*

The seasonal developmental state of the phytoplankton following the initiation of the spring bloom, was indirectly described by the consumption of nitrate since bloom initiation (Naustvoll et al., this issue).

The nitrate present after the winter mixing minus the amount left at the time of sampling were presumed to represent the cumulative phytoplankton growth since the initiation of the spring bloom (Naustvoll et al., this issue). The cumulative phytoplankton growth was inversely related to the depth of the mixed layer (Fig. 2), the latter taken from Drinkwater et al., (this issue). In Strand et al. (this issue), it was shown that the numbers of copepodite stage five (CV) and adults (CVI) of *Calanus finmarchicus* peaked in waters with low levels of nitrate depletion, i.e. which correspond to the pre-bloom phase (Fig. 3). This is in accordance with previous investigations of the Norwegian Sea (Bagøien et al., 2012; Broms and Melle, 2007; Broms et al., 2012, 2009; Stenevik et al., 2007). Thus, the trans-Atlantic survey highlights the functional relationship between the shallowing of the mixed layer caused by the stabilisation of the water column that facilitates phytoplankton biomass increase and the development of the spring phytoplankton bloom (Sverdrup, 1953), and further documented that the occurrence of the G0 in stages CV and CVI coincided with the pre-bloom at low levels of nitrate depletion across the Atlantic (Strand et al., this issue). The interannual and spatial variability in the timing of the water column stabilisation (Rey, fx22004), therefore is the physical driver of the phenology of both phyto- and zooplankton production.

In the Norwegian Sea, it was previously shown that herring co-occur with low levels of nitrate depletion during the pre-bloom (less than 0.2 mol m^{-2} in Fig. 3) when the numbers of CV and CVI of *C. finmarchicus*, peak (Broms et al., 2012). The CV and CVI present during the pre-bloom were assigned to the overwintering generation of *C. finmarchicus*, recently ascended from the overwintering depths to the surface. It was concluded that the herring represented the third trophic level functionally related to the factors that trigger the spring bloom (Broms et al., 2012). During the present cruise, the herring were present in relatively low numbers during what was interpreted as a late-bloom period. It was concluded that these herring did not have optimal feeding conditions and were probably lagging the front of the herring migration (Melle et al., this issue). The herring do not enter the Irminger and Labrador seas, although our analysis indicates that there might be a "herring feeding window" as indicated by the low nitrate consumption values and high CV and CVI abundances of G0. The reason for this could be that in the Irminger and Labrador seas there are no suitable spawning grounds for the herring from where it could reach the "herring feeding window" after spawning.

It is likely, however, that there are other zooplanktivorous populations in those seas that take advantage of this pre-bloom peak in abundance and biomass of large and fat individuals of recently ascended *C. finmarchicus*. Who would they be? Based on the abundance and distribution data analysed in Strand et al. (this issue) and Klevjer et al. (2020a), the macrozooplankton and mesopelagic micronekton together with the large *Scyphozoa* are always present and can migrate into the surface layers to feed during night-time. Migratory species that would be able to follow the peak of G0 as its location shifts during the bloom development (Broms et al., 2012), would probably be seabirds and whales. Nevertheless, the Labrador and Irminger seas are not inhabited by large stocks of horizontally migrating pelagic fish taking advantage of the phenological signal described here, as they do in the Norwegian and Iceland seas. This is discussed in more detail below.

3.3. Size structures of the pelagic communities

Information about the size structure of the pelagic communities in the four seas came from several types of equipment. Biomass and abundance data from net hauls showed that the biomass (dry weight) of the smallest size fraction was highest in the Norwegian Sea (Strand et al., this issue), but the only significant difference in the biomasses was the high biomass of the larger than 2 mm fraction in the Icelandic Sea. The results from the high-resolution optical sensors (OPC, VPR) gave a somewhat different impression (Strand et al., this issue). While the OPC results also indicated that the densities of small particles peaked in the Norwegian Sea, the OPC results showed a high biovolume of intermediate sized particles (1–3 mm ESD) in the surface near waters in the western basins, especially the Labrador Sea (Fig. 4). In the areas with the high OPC biovolumes, the VPR documented the presence of relatively high densities of gelatinous plankton. Biovolume to dry-weight ratios of crustacean and gelatinous plankton are very different (e.g. Kiørboe, 2013), which may be one explanation for why high biovolumes of particles observed with the OPC did not translate into high dry weights in the plankton nets. In the same area, we also observed high densities of *Phaeocystis* colonies (Naustvoll et al., this issue) with a range of diameters from 1.5 to 6 mm, which fit into the observed ESD range. These colonies would largely disintegrate and pass through the 180 μm screen, not adding much to the plankton biomass.

The larger size fractions of the micronekton (> 10 g) were absent in the trawl catches from the Norwegian and Iceland seas (Klevjer et al., 2020a). The micronekton size distributions in the Norwegian and Iceland seas were therefore truncated towards bigger sizes when compared to the western basins (Fig. 4). Both western basins also had large wet-weights of large mesopelagic *Scyphozoa* in the trawl catches. Though the same species are known to occur in the eastern basins, the average weights caught there were much lower (Table 1). The differences in size distributions and taxonomy among the seas may suggest the presence of an alternative trophic pathway in the western basins (Klevjer et al., 2020a).

3.4. Vertical distributions and light regimes across the North Atlantic

The vertical distribution, when measured in terms of depth, was very different between the areas (Klevjer et al., 2020b), and the depth of the peak mesopelagic backscattering varied from about 550 m in the Irminger Sea to about 250 m in the Labrador Sea. Analysis however showed that the vertical distribution of the DSL's was linked to a common light level across the Atlantic, with the vertical distribution of DSLs tracking a "preferred" light level closely (Klevjer et al., 2020b). In all basins diffuse attenuation coefficients in surface waters were strongly dependent on *in situ* chlorophyll levels (Klevjer et al., 2020a). As a consequence of the high chlorophyll levels in the Labrador Sea (Klevjer et al., 2020b), attenuation levels there were much higher than seen in the other seas, and the depth distribution of backscatter was "abnormal", with much of the mesopelagic backscatter found from 200 to 300 m depth, several hundred meters shallower than in the neighbouring Irminger Sea (Klevjer et al., 2020b). As the cruise extended into high latitudes in the Arctic summer, night-time surface irradiance maxima also spanned orders of magnitude (Norheim et al., 2016). In the Iceland Sea night-time estimated light levels in the epipelagic were higher than the preference level, and the DVM of the organisms from the DSL did not reach epipelagic depths (Norheim et al., 2016; Klevjer et al., 2020b). Light level at depth is the product of both in water attenuation and surface irradiance, and as the cruise covered a wide range of latitudes, with varying cloud coverage and high variation in the in-water attenuation levels, *in situ* light levels at depth varied extensively. Previous work has suggested that on a global scale daytime peak backscattering level of the DSL is highly correlated with *in situ* light levels (Aksnes et al., 2017) and the same pattern is evident in the data from our Euro-BASIN cruise (Klevjer et al., 2020a).

3.5. Vertical connectivity

In all basins, the vertical distribution of organisms in the mesozooplankton size range (0.2–20 mm) was skewed towards the surface, regardless of time of day (Strand et al., this issue), with generally low fractions of biomass found beyond 200 m depth. Despite the surface oriented distribution of biomass in the mesozooplankton group, we observed signals of DVM, especially in the data from the sensors deployed on the tow-body MESSOR (Strand et al., this issue; Melle et al., this issue). These data show distributions consistent with "normal"

DVM, with relatively deeper distribution during the day, and migration to shallow habitats during night, in the Norwegian Sea. In the Iceland Sea, there was little difference between the day and night vertical distributions of mesozooplankton during the May transit, suggesting limited DVM at that time. Cessation of, or low amplitude, DVM activity for mesozooplankton during the Arctic summer is apparently a frequent occurrence (Dale, 2000; Blachowiak-Samolyk et al., 2006). At these latitudes and during this period of the year, darkness is limited to only a few hours, and light levels even at the darkest hours are several orders of magnitude brighter than farther south (Norheim et al., 2016). Such special light regimes may lead to altered DVM behaviour in the trade-off between surface foraging and at-depth predator avoidance.

During the high summer, on our return trip, the field data suggested that DVM for larger components of mesozooplankton had resumed in the Iceland Sea (or at least in the frontal area between the Norwegian and Iceland Seas; Melle et al., this issue), despite higher night-time light levels and even shorter nights during this time. Chlorophyll levels were higher at this time so the conditions for herbivorous feeding close to the surface may have been better, though total densities of larger mesozooplankton were down, so feeding conditions for predatory plankton may have been worse. The higher chlorophyll levels in surface waters also mean a relative deterioration in visual ranges for planktivorous fish (Melle et al., this issue). Both "drivers" and "deterrents" for the DVM trade-off were therefore likely to have changed compared to the outbound leg.

To quantify some of these effects, we parameterized a model for aquatic visual feeding (; Varpe and Fiksen, 2010) based on measurements of optical conditions made during the cruise (Klevjer et al., 2020b; Melle et al., this issue). The results (Fig. 6) document a significant drop (~0.5x) in potential search volume for a visually feeding planktivore in the Iceland Sea on the return trip, highlighting that there would have been a change in the vertical distribution of predation risk, one running counter to that expected from the seasonal solar cycle, for the Iceland Sea over the course of the cruise (Melle et al., this issue).

In the western basins, the available data from the cruise suggest that the mesozooplankton adopted a reverse DVM strategy during the cruise, i.e. with a deep distribution during night, and a shallow distribution during the day. In the OPC data from the Labrador Sea, we measured a net loss of biovolume at shallow depths during night, with corresponding increases at depth (Strand et al., this issue). Reverse migration strategies for mesozooplankton have previously been linked to conditions where vertically migrating, non-visual predators are important (Ohman et al., 1983), but could also be expected for prey avoiding zooplanktivores with ordinary DVM, such as mesopelagic fishes, hiding at depth during daytime. The biomass of mesopelagic Scyphozoa (*Periphylla periphylla*, a known vertical migrator (Klevjer et al., 2009) and *Atolla* sp.) was much higher in the western basins, and data from the Video Plankton Recorder (Strand et al., this issue) also documented relatively high densities of smaller gelatinous plankton in the west, so biomass of non-visual predators were higher in the western areas. Further, the absence of schooling epipelagic fish in the west (Klevjer et al., 2020a), suggested that the predation pressure from these visual predators also was lower in the western areas during daytime. On the other hand, the hull-mounted acoustic data together with the trawl catches suggest a larger biomass of mesopelagic fish entering the epipelagic during night-time in the western areas (Table 1). In summary, the catch and acoustic data point towards the existence of a gradient in the importance of daytime visual predation from east to west, and with non-visual, and likely night-time visual, predation relatively more important in the western basins. In line with what can be expected under these conditions we observed reverse migration of mesozooplankton in the western Atlantic, but we do not know whether reverse migrations are the norm or somehow connected with the extreme vertical distribution of other components during the survey (see section on micronekton).

One major structural difference between the eastern and western basins was that in the eastern basins a very high proportion of backscatter in the DSL's appeared to migrate, whereas in the western basins only a small decrease in the proportion of backscatter occurred at night, suggesting that a much lower proportion of DSL inhabitants participated in DVM in the western basins (Klevjer et al., 2020a,b this issue a, this issue b). On a global scale, the migrating proportion of backscatter has been found to link closely to midwater oxygen levels (Klevjer et al., 2016), with a high proportion of DSL backscatter migrating when oxygen values were low or under oxygen strain due to higher temperature (Klevjer et al., 2012). Since all basins covered during this study have high oxygen levels and relatively low temperatures, the migration patterns observed during the Euro-BASIN cruise are linked to downwelling light as the primary environmental driver.

The eastern basins are mainly inhabited by a few, highly (vertically) migratory species of mesopelagic fish, whereas the western basins have a much higher diversity, also including species normally considered vertically non-migratory (Klevjer et al., 2020b). As the potential for dispersion between the western and the eastern basins is likely to be high (e.g. they are "downstream", with large surface transport into the eastern area), one can pose the question "why are mesopelagic resident fish individuals/species (relatively) absent from the Norwegian and Iceland Seas"? Even if the absolute migrating and resident biomasses are hard to estimate from acoustics alone, the differences in migrating proportion of backscatter across the Atlantic are striking (Klevjer et al., 2020b), and are likely to have severe consequences for active transport of carbon to depth, as our estimates suggest that during our cruise, the biomass of dielly migrating micronekton may have exceeded that of dielly migrating mesozooplankton in the western basins.

3.6. Vertical connectivity and mesopelagic biomass

Energy input to mesopelagic ecosystems comes either via active or passive flux, since there is no primary production at these depths. Our data suggest that the western mesopelagic biomasses are maintained on a higher active micronektonic flux than in the eastern basins, even if our relative values of the flux based on acoustics may be underestimated in the east (Table 1). Energy can also be brought into the mesopelagic zone by DVM of smaller (e.g. mesozooplankton) components. Even if these mesozooplankton fluxes were detectable in our data (e.g. Strand et al., this issue), the vertical distributions of plankton show that at the time of the survey of the 4 basins, much of the mesozooplankton biomass was associated with near surface waters regardless of time of day. Based on day to night changes in OPC biovolume (Strand et al., this issue) estimates of diel changes in the 200-0 m depth range span 45% (NS) to 11% and 12% in ICS and IRS, with LS (19%) at intermediate levels. If these estimates are correct, they would translate to (see Table 1) a migrant biomass of ~0.2 g C m^{-2} d^{-1} (between epi- and mesopelagic) in all basins except the NS, where the migrant mesozooplankton biomass would be ~0.7 g C $m^{-2}d^{-1}$. Our estimates suggest that both magnitude and the relative importance of the mesozooplankton active flux is highest in the Norwegian Sea.

Given that the Norwegian Sea is the basin with the highest potential daytime predation pressure from visual predators (e.g. from horizontally migrating epipelagic fish), the pronounced DVM of mesozooplankton in NS makes ecological sense. However, the higher mesopelagic biomass found in the western basins shows that more carbon is retained at mesopelagic depths there. Barring huge differences between the areas in carbon content in the DOC and bacterial pools at mesopelagic depths, this also implies that overall more carbon is metabolized there, just to cover the basal metabolism of the micronektonic components, at the higher temperatures (e.g. Drinkwater et al., this issue; Klevjer et al., 2020b) found in the western basins. Since primary production levels and primary producer taxonomy/sizes (Naustvoll et al., this issue) are not that dissimilar, with the overall lowest estimated new and total primary productivity found in the basin with the highest mesopelagic micronektonic biomass (Table 2), this implies that energy flows in the pelagic

food-webs are significantly different between the eastern and western basins.

We're currently unable to fully quantify the processes with which this carbon is taken up or retained by the mesopelagic components. Our estimates of active transport suggest that for micronekton this mechanism is 3–4 times larger in the Labrador and Irminger seas than in the Norwegian Sea, while for mesozooplankton the transport is highest in the Norwegian Sea. Results from the southern hemisphere have highlighted that the relationship between backscatter and biomass is unlikely to be the same across different latitudes (Escobar-Flores et al., 2018; Dornan et al., 2019), and the acoustic patterns and trawled biomasses across the 4 basins (Klevjer et al., 2020a) also show that the assumption of similar acoustic properties across the basins is unlikely. If we use the acoustically migrating proportion to estimate migrating biomasses based on biomass levels from the trawl catches, the resulting estimates put micronekton gut flux as a major transport pathway for carbon into the mesopelagic zone. In the western basins, this also leads us to estimate that the migrating micronekton biomass exceeds the migrating mesozooplankton biomass (Table 1). Using back-of-the-envelope calculations, Angel (1985) estimated 2.5 mg C d^{-1} in gut flux, i.e. directly transported and defecated-at-depth carbon, per 1 g WW of migrating fish biomass. Combining this estimate with our estimates of migrating fish biomass would suggest that mesopelagic fish carbon gut flux in the basins could range from 6.9 mg C m^{-2} d^{-1} in LS, 5.5 mg C m^{-2} d^{-1} in IRS, to 2.0 mg C m^{-2} d^{-1} in NS and 0.2 mg C m^{-2} d^{-1} in ICS. Better attempts at modelling micronekton contribution to vertical carbon flux exist, and also take into account other important processes such as respiration, mortality etc. (Davison et al., 2013; Hudson et al., 2014), but in general attempts at understanding the influence of micronekton on vertical transport are hampered by lack of data on large-scale distribution of both biomass and migration patterns (e.g. Irigoien et al., 2014; Klevjer et al., 2016).

Accurately assessing the gut flux would require more information, but if we assume that our estimates of migrating biomass and transport are approximately correct and are constant over the year, the active flux through gut transport would be ~2.5 g C m^{-2} yr^{-1} in LS, 2 g C m^{-2} yr^{-1} in IRS, 0.7 in NS and 0.1 g C m^{-2} yr^{-1} in ICS. This is about equal to the estimated carbon content of the mesopelagic micronekton in all basins except the Norwegian Sea, where the estimated gut flux equals ~10x the carbon content of the teleost micronekton, again highlighting the likely high importance of active transport to sustain the mesopelagic biota in the Norwegian Sea.

Passive flux is the other important process that brings particulate carbon to mesopelagic depths. We did not focus on estimating the magnitude of the passive flux during the cruise, but maximum densities of marine snow particles recorded by the VPR (Strand et al, this issue) were at least 1 order of magnitude higher in the deployments in the western areas. Additionally, data from fluorometers on both the CTD and the MESSOR tow-body documented spikes of fluorescence at depth in the Labrador Sea, suggesting that phytoplankton were in the process of rapidly sinking out in this region (Naustvoll et al., Strand et al., this issue). Since deployments of the tow-body (and thereby VPR data) in both the Labrador and Irminger Seas were at least partially in areas with phytoplankton bloom conditions, we do not know whether the VPR observations of marine snow represents "typical" conditions, or reflect the bloom conditions in the epipelagic above. Satellite chlorophyll data document that the spring blooms in the different areas have different magnitudes, with much higher chlorophyll levels typically recorded in the Labrador Sea (Naustvoll et al., this issue) than in the other areas, and with very similar annual cycles of average chlorophyll levels found in the Irminger and Norwegian seas. The lack of a pronounced peak in spring bloom chlorophyll levels in the Norwegian Sea has previously been associated with the effects of mesozooplankton grazing (e.g. Bodungen et al., 1995; Rey, 2004). If mesozooplankton grazing restricts phytoplankton build-up in the Norwegian and Irminger Seas, while it is unable to keep abreast of the phytoplankton growth in the Labrador Sea, we assume that faecal pellets will be more important to the total passive vertical flux in the first case, while individual algal cells and aggregates should be overall more important in the second. Since the nature of the sinking particle also typically affects its sinking speed (Turner, 2015), it is likely that total passive carbon flux is affected differently in the three areas.

Our data do not allow us to estimate the annual vertical export or the annual pattern of export for the different areas. However, even if the passive carbon flux was 1 order of magnitude higher in the western areas, most mesopelagic micronekton do not feed on passively sinking material directly, they feed on mesozooplankton feeding on the detritus. There is no indication in the vertical distribution of mesozooplankton biomass to suggest that mesozooplankton biomasses at depth are higher in the western basins (Strand et al., this issue), in fact the data show that a slightly higher proportion of total mesozooplankton biomass 1000-0 m is found at mesopelagic depths in the eastern basins (Fig. 7, Row C). It could be argued that this could be an effect of increased predation pressure on mesopelagic plankton in the western basins. To provide answers on the importance of the passive flux for maintaining mesopelagic biomasses, depth-resolved (including mesopelagic) estimates of mesozooplankton production levels are needed, as mesozooplankton feature heavily in the diet of many micronektonic species (Drazen and Sutton, 2017). Current efforts at modelling biomasses of mesopelagic micronekton must tune parameters to values that would be unlikely for epipelagic species (e.g. Irigoien et al., 2014; Anderson et al., 2019) in order to reconcile estimates of mesopelagic biomass with modelling output. Our results therefore highlight the need for more focused studies on basic rates, production levels, and trophic interactions of mesopelagic components to understand actual energy flows in open ocean ecosystems.

3.7. Pelagic ecology across the atlantic

Regardless of which carbon pool the mesopelagic components draw their energy from, the carbon requirements of the mesopelagic micronektonic components comes in addition to those of the other organisms in the water column, in a zero-sum game bounded by the levels of ecosystem productivity. Epipelagic and upper mesopelagic, schooling fish were only detected acoustically in the eastern basins (Klevjer et al., 2020a). It is well known that the Norwegian and Iceland seas are home to several large pelagic zooplanktivorous stocks, such as herring, mackerel, blue whiting (*Micromesistius poutassou*), and capelin that use these seas for foraging (Skjoldal, 2004). It is interesting that stocks of many of these species, e.g. mackerel, herring, and capelin, can be found on both the eastern and western sides of the Atlantic, but that we only observed representatives in the eastern basins during the cruise.

It is not likely coincidental that the basins with low mesopelagic biomass also are the basins with large stocks of "other" planktivorous components, either epipelagic (e.g. herring, mackerel) or mesopelagic (e.g. blue whiting). At present, we do not know which factor is the cause and which the effect, but we will in the following discuss factors that possibly contribute to the observed patterns.

3.8. Potential causes for and paradoxes of the observed patterns

Different primary productivity, but also competition between different planktivorous components are potential explanations for the observed patterns of micronektonic and nektonic biomass across the basins. The only significant difference found in mesozooplankton standing stocks during the cruise was the higher biomass in the large fraction (> 2 mm) found in the Iceland Sea. In this area, the vertical migration of mesopelagic micronekton was restricted vertically during the cruise (Norheim et al., 2016), the increased densities of larger mesozooplankton could therefore be interpreted as an effect of reduced predation. However, there is also a general trend of increasing body size with decreasing temperatures globally (Martin et al., 2006; Chiba et al.,

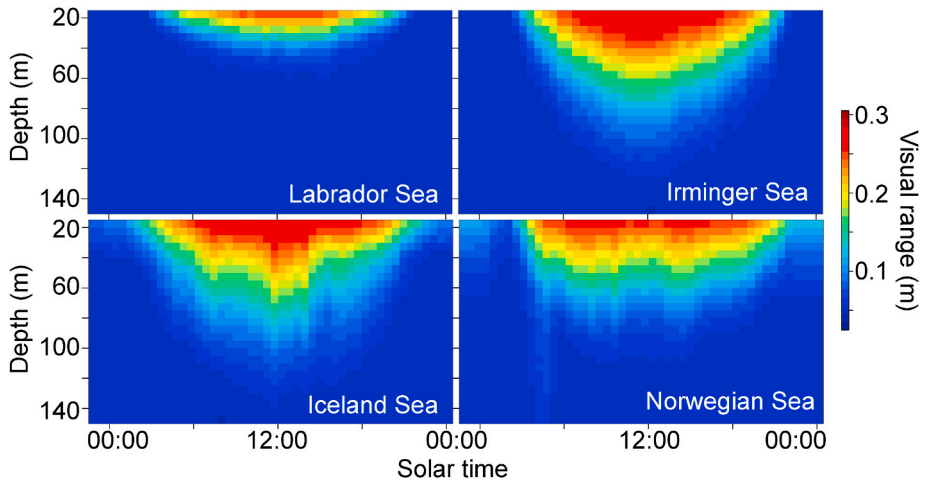

Fig. 5. Theoretical visual range: Per basin estimated visual ranges averaged over diel cycles for a modelled herring searching for *Calanus* type particles, based on modelled *in situ* light levels and beam attenuation. Figures show average conditions during the basin crossings of the Euro-BASIN survey. See APPENDIX A for details on the methods.

2015), which may confound this interpretation. The high biomass of the large Arctic copepod *C. hyperboreus* found in the large size fraction in the Iceland Sea, as well as the much higher biomass to abundance ratio of chaetognaths found in the Iceland Sea compared to the Norwegian Sea, supports this. As mentioned, the size distributions of micronekton in the eastern basins were truncated, and this "size-niche" may possibly be taken by the horizontally migrating nekton in the eastern basins. We also estimate 3–4 times higher biomass of fish entering the epipelagic from mesopelagic depths during night in the western seas, and scyphozoan biomass was also higher (Tables 1 and 2). Thus, the epi-pelagic fish stocks would meet a much higher degree of competition for food in the west. However, we are unable to answer whether the horizontal migrators are largely lacking from the western basins because they are outcompeted, or that they are outcompeting most mesopelagic components in the east. Even though the pelagic fish stocks of the eastern basins represent huge biomasses, their presence in the open seas is seasonal, and their prey consumption is low due to lower P/B ratio (Skjoldal, 2004), even though the biomass per m^{-2} ocean surface is substantial compared to mesopelagic biomasses (Table 2). This may suggest that competition from the mesopelagic components has more impact on the epi-pelagic fish stocks than *vice versa*.

Based at least partially on observed north-south gradients of mesopelagic biomass in the Norwegian Sea, a hypothesis has been presented that the high-latitude light-climate effectively limits stock sizes of mesopelagic visual predators at high latitudes (Kaartvedt, 2008). In practice, the predictions of this hypothesis, which are consistent with effects observed in Norheim et al. (2016) and Klevjer et al. (2020b) (this issue b), would give the horizontally migrating epipelagic fish unrestrained access to the epipelagic resources during summer (Melle et al., this issue), and is likely to be a contributing factor to their relative success in the Iceland and Norwegian Seas. It could be that the mesopelagic planktivores, either through the constant cropping of zooplankton, through indirect effects caused by strengthening of zooplankton DVM behaviour, or through predation effects on eggs and larvae (see below), prevent epipelagic planktivores from dominating the systems.

Effects of predation could also potentially explain the observed patterns. The epipelagic (and/or larger nektonic) stocks are predators on the mesopelagic species, and it is possible that they are keeping them at reduced biomass levels in the east. We know that mesopelagic micronekton and macroplankton are important components in the diet of the stocks of the larger mesopelagic nekton such as blue whiting, and that their eggs and larvae may occur in the diets of herring and mackerel (Skjoldal, 2004; Dalpadado et al., 2000; Bachiller et al., 2016; Prokopchuk and Sentyabov, 2006). However, if epipelagic species are capable of reducing the biomass of the mesopelagic fish in the Norwegian Sea, why are these or other species not utilizing the same niche in the Irminger and Labrador Seas? Alternatively, many of the mesopelagic species, including the scyphozoans, are predators on larvae and eggs of epipelagic species. Since pre-recruitment mortality is a major factor in regulating the stock-sizes of epipelagic species, it is not impossible that predation from mesopelagic components hinders the establishment of epipelagic stocks in the western basins, but again we lack information that would allow us to answer "which direction" of predation is the more important.

Zooplankton biomass in the upper 200 m were relatively similar between the areas, and *Calanus finmarchicus* numerically dominated the mesozooplankton size-fraction in all basins (Strand et al., this issue; Melle et al., this issue). However, biomass alone may be a poor predictor of food availability, and e.g. optical conditions will also affect ecological interactions and food intake. We modelled (; Melle et al., this issue, see Appendix A) visual ranges for an epipelagic planktivore, and the results highlight that the high diffuse attenuation coefficients in the Labrador Sea during the survey decreased the potential for visual planktivory in this area. We found that in the Labrador Sea, modelled visual ranges for a herring type fish feeding on a *Calanus* type prey were very small except from a very narrow strip close to the surface (Fig. 5). Over the course of a full diel cycle, this has large implications for the total potential volume searched (Fig. 6). On the westward leg the calculated daily search volume for a 30-cm herring swimming at 32.5 m depth at 2 BL s^{-1} ranged from 515 m^{-3} d^{-1} in the Labrador Sea (near continental shelf) to 3450 m^{-3} d^{-1} in the Iceland Sea. Both the Norwegian Sea (3260 m^{-3} d^{-1}) and the Irminger Sea (2865 m^{-3} d^{-1}) had values considerably higher than the Labrador Sea. On the eastward survey, calculated values for the Irminger had similar magnitude (2475 m^{-3} d^{-1}), while we estimated higher values for the central Labrador Sea (905 m^{-3} d^{-1}) compared to the values close to the shelf on the westward survey. Despite the eastward survey occurring closer to the summer solstice, we estimated lowered clearance efficiencies in the Iceland Sea (1685 m^{-3} d^{-1}), highlighting that clearance efficiencies are likely to be heavily influenced by weather and *in situ* optical conditions, in addition to the seasonal solar cycle. The profitability of an area as a feeding ground for epipelagic planktivorous stocks probably depends on the "match" between the phenology of the plankton prey, the available horizontal planktivore routes (migration between spawning and feeding areas) and the environmental (e.g. optical, current, temperature) regime. Some of these factors may be constrained by organism life cycle or physiology (e.g. due to location of spawning, overwintering areas, temperature

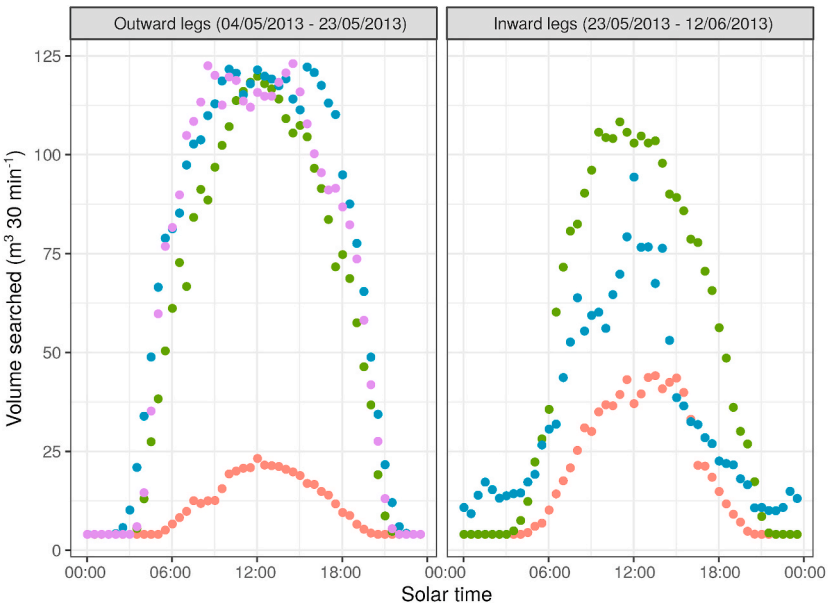

Fig. 6. Diel cycle in theoretical visual range: Basin averages of estimated volume (m^3) searched per 30 min interval ("clearance efficiency") for a herring swimming with 2 body-lengths (BL) s^{-1} at 32.5 m depth, plotted against time of day (solar time) for the 4 basins. Left panel: westward legs (before 23.05.2013), right panel eastward leg (after 23.05.2013). Norwegian Sea background data, e.g. surface reference light and CTD's from the eastern parts of the return trip are lacking and were therefore not computed. See APPENDIX A for details on methods.

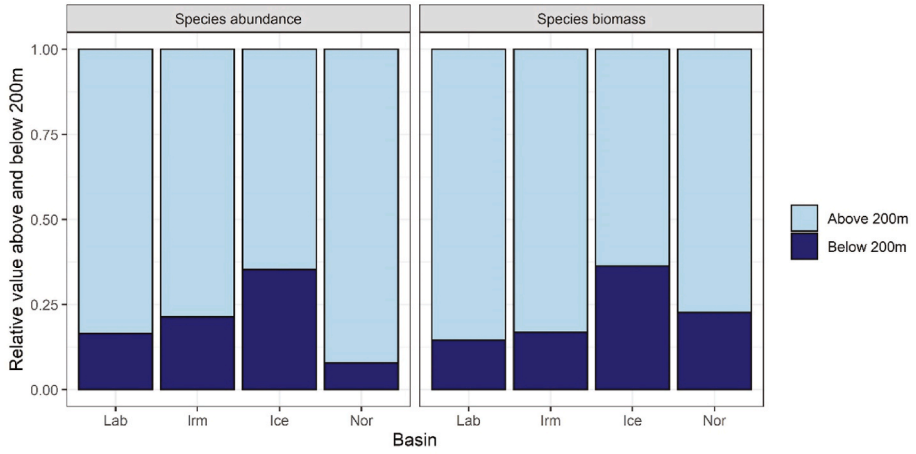

Fig. 7. Measured species abundance (left) and backcalculated biomass (right) from species/stage literature values of prosome-lengths for different species (Strand et al., this issue) separated into vertical position above and below 200m. Note that important groups like Chaetognaths are omitted since biomass cannot be estimated from abundance data.

ranges), and their combination may make some areas "unavailable" or unprofitable to epipelagic migrating stocks.

Ultimately, all levels of the food-web are fed by the carbon fixed by the primary producers. In some Norwegian fjords biomass levels of mesopelagic fish have been found to be inversely related to the biomass of mesopelagic jellyfish (Eiane et al., 1999; Aksnes et al., 2009) consistent with mesozooplankton productivity being shunted into a "gelatinous" versus a "teleost" food-web (Haraldsson et al., 2012; Schnedler-Meyer et al., 2016). The controlling factor in these studies are attributed to optical conditions causing persisting reduced visibility that favours tactile feeders like jellyfish rather than visually foraging fish. Similarly, the reduced visibility in the Labrador Sea might imply that the gelatinous organisms are favoured on the behalf of fishes (Fig. 5). Gelatinous organisms were indeed abundant both in the VPR data (Strand et al., this issue) and trawl catches (Klevjer et al., 2020a) from the Labrador Sea. However, it is unclear to what extent the reduced visibility in the Labrador Sea is a permanent feature precluding fishes, or only temporarily connected to the more intensive bloom observed at the time of the cruise. Furthermore, while *Scyphozoa* wet-weights were 15 times higher in the Labrador Sea catches than in the Norwegian Sea, so was the biomass of the mesopelagic fishes (Klevjer et al., 2020a). Also, *Scyphozoa* biomass was even higher in the Irminger Sea, which had both very clear water (Fig. 5) and the highest biomasses of mesopelagic fish of any area (Klevjer et al., 2020a). Jellyfish are both competitors and potential predators on most planktivorous marine fish (or at least their eggs and larvae) (Purcell and Arai, 2001; Purcell et al., 2007). It may therefore be a paradox that in the catches from the Euro-BASIN cruise there is a positive correlation between teleost and gelatinous biomass. Despite the presumed competitive relationship such positive correlation could have been explained by higher primary production (Haraldsson et al., 2012; Schnedler-Meyer et al., 2016). However, the Irminger Sea, which by far had the lowest primary production (Table 2), provided the highest total biomass of zooplanktivores. This suggests that for the large-scale patterns of the open ocean of the North Atlantic, the apparent food web transfer as well as the competition between gelatinous and teleost organisms are masked by other stronger interactions.

CRediT authorship contribution statement

Webjørn Melle: Conceptualization, Formal analysis, Investigation,

Writing - original draft, Writing - review & editing, Visualization, Project administration, Funding acquisition. **Thor Klevjer:** Conceptualization, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization, Funding acquisition. **Kenneth F. Drinkwater:** Conceptualization, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **Espen Strand:** Conceptualization, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **Lars Johan Naustvoll:** Conceptualization, Formal analysis, Investigation, Writing - review & editing. **Peter H. Wiebe:** Conceptualization, Formal analysis, Investigation, Writing - review & editing. **Dag L. Aksnes:** Conceptualization, Formal analysis, Investigation, Writing - review & editing. **Tor Knutsen:** Conceptualization, Formal analysis, Investigation, Writing - review & editing. **Svein Sundby:** Conceptualization, Formal analysis, Investigation, Writing - review & editing. **Aril Slotte:** Conceptualization, Formal analysis, Investigation, Writing - review & editing. **Nicolas Dupont:** Conceptualization, Formal analysis, Investigation, Writing - review & editing. **Anne Gro Vea Salvanes:** Conceptualization, Formal analysis, Investigation, Writing - review & editing. **Rolf Korneliussen:** Conceptualization, Formal analysis, Investigation, Writing - review & editing. **Geir Huse:** Conceptualization, Investigation, Writing - original draft, Writing - review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr2.2020.104838.

References

Aksnes, D., Dupont, N., Staby, A., Fiksen, Ø., Kaartvedt, S., Aure, J., 2009. Coastal water darkening and implications for mesopelagic regime shifts in Norwegian fjords. Mar. Ecol. Prog. Ser. 387, 39–49. https://doi.org/10.3354/meps08120.

Aksnes, D.L., Røstad, A., Kaartvedt, S., Martinez, U., Duarte, C.M., Irigoien, X., 2017. Light penetration structures the deep acoustic scattering layers in the global ocean. Sci. Adv. 3 https://doi.org/10.1126/sciadv.1602468 e1602468. https://search.crossref.org/?q=Aksnes%2C+D.L.%2C+R%C3%B8stad%2C+A.%2C+Kaartvedt%2C+S%2C+Martinez%2C+U.%2C+Duarte%2C+C.+M.%2C+Irigoien%2C+X.%2C+2017.+Light+penetration+structures+the+deep+acoustic+scattering+layers+in+the+global+ocean.+Sci.+Adv.+3%2C+e1602468.

Anderson, T.R., Martin, A.P., Lampitt, R.S., Trueman, C.N., Henson, S.A., Mayor, D.J., 2019. Quantifying carbon fluxes from primary production to mesopelagic fish using a simple food web model. ICES J. Mar. Sci. 76 (3), 690–701. https://doi.org/10.1093/icesjms/fsx2342019.

Angel, M., 1985. Vertical migrations in the oceanic realm: possible causes and probable effects. In Migration : mechanisms and Adaptive Significance. In: Rankin, M.A. (Ed.), Contrib. Mar. Sci. 27, 27–45.

Astthorsson, O.S., Valdimarsson, H., Gudmundsdottir, A., Óskarsson, G.J., 2012. Climate-related variations in the occurrence and distribution of mackerel (*Scomber scombrus*) in Icelandic waters. ICES J. Mar. Sci. 69, 1289–1297. https://doi.org/10.1093/icesjms/fss084.

Bachiller, E., Skaret, G., Nøttestad, L., Slotte, A., 2016. Feeding ecology of Northeast Atlantic mackerel, Norwegian spring-spawning herring and blue whiting in the Norwegian Sea. PloS One 11 (2). https://doi.org/10.1371/journal.pone.0149238 e0149238.

Bagøien, E., Melle, W., Kaartvedt, S., 2012. Seasonal development of mixed layer depths, nutrients, chlorophyll and Calanus finmarchicus in the Norwegian Sea - a basin-scale habitat comparison. Prog. Oceanogr. 103, 58–79.

Barrett, R.T., Chapdelaine, G., Anker-Nilssen, T., Mosbech, A., Montevecchi, W.A., Reid, J.B., Veit, R.R., 2006. Seabird numbers and prey consumption in the North Atlantic. ICES J. Mar. Sci. 63 (6), 1145–1158. https://doi.org/10.1016/j.icesjms.2006.04.004.

Blachowiak-Samolyk, K., Kwasniewski, S., Richardson, K., Dmoch, K., Hansen, E., Hop, H., Falk-Petersen, S., Mouritsen, L.T., 2006. Arctic zooplankton do not perform diel vertical migration (DVM) during periods of midnight sun. Mar. Ecol. Prog. Ser. 308, 101–116.

Bodungen, B., Antia, A., Bauerfeind, E., Haupt, O., Koeve, W., Machado, E., Peeken, I., Peinert, R., Reitmeier, S., Thomsen, C., Voss, M., Wunsch, M., Zeller, U., Zeitzschel, B., 1995. Pelagic processes and vertical flux of particles: an overview of a long-term comparative study in the Norwegian Sea and Greenland Sea. Geol. Rundsch. 84, 11–27. https://doi.org/10.1007/bf00192239. In: https://search.crossref.org/?q=Bodungen%2C+B.%2C+Antia%2C+A.%2C+Bauerfeind%2C+E.%2C+Haupt%2C+O.%2C+Koeve%2C+W.%2C+Machado%2C+E.%2C+Peeken%2C+I.%2C+Peinert%2C+R.%2C+Reitmeier%2C+S.%2C+Thomsen%2C+C.%2C+Voss%2C+M.%2C+Wunsch%2C+M.%2C+Zeller%2C+U.%2C+Zeitzschel%2C+B.%2C+1995.+Pelagic+processes+and+vertical+flux+of+particles%3A+an+overview+of+a+long-term+comparative+study+in+the+Norwegian+Sea+and+Greenland+Sea.+Geol.+Rundsch.+84%2C+11%E2%80%9327.

Broms, C., Melle, W., 2007. Seasonal development of *Calanus finmarchicus* in relation to phytoplankton bloom dynamics in the Norwegian Sea. Deep-Sea Res. Part II 54, 2760–2775.

Broms, C., Melle, W., Kaartvedt, S., 2009. Oceanic distribution and life cycle of *Calanus* species in the Norwegian Sea and adjacent waters. Deep-Sea Res. Part II 56, 1910–1921.

Broms, C., Melle, W., Horne, J.K., 2012. Navigation mechanisms of herring during feeding migration: the role of ecological gradients on an oceanic scale. Mar. Biol. Res. 8, 461–474.

Chiba, S., Batten, S.D., Yoshiki, T., Sasaki, Y., Sasaoka, K., Sugisaki, H., Ichikawa, T., 2015. Temperature and zooplankton size structure: climate control and basin-scale comparison in the North Pacific. Ecol. Evol. 5, 968–978. https://doi.org/10.1002/ece3.1408.

Dale, T.K., 2000. Diel patterns in stage-specific vertical migration of *Calanus finmarchicus* in habitats with midnight sun. ICES J. Mar. Sci. 57, 1800–1818. https://doi.org/10.1006/jmsc.2000.0961.

Dalpadado, P., Ellertsen, B., Melle, W., Dommasnes, A., 2000. Food and feeding conditions of Norwegian spring-spawning herring (Clupea harengus) through its feeding migrations. ICES J. Mar. Sci. 57, 843–857.

Davison, P.C., Checkley Jr., D.M., Koslow, J.A., Barlow, J., 2013. Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. Prog. Oceanogr. 116, 14–30.

Dornan, T., Fielding, S., Saunders, R.A., Genner, M.J., 2019. Swimbladder morphology masks Southern Ocean mesopelagic fish biomass. Proc. R. Soc. B. Biol. Sci. 286, 20190353.

Drazen, J.C., Sutton, T.T., 2017. Dining in the deep: the feeding ecology of deep-sea fishes. Annu. Rev. Mar. Sci. 9, 337–366. https://doi.org/10.1146/annurev-marine-010816-060543.

Drinkwater, K. F., Sundby, S., Wiebe, P. Exploring the hydrography of the boreal/arctic domains of North Atlantic seas: results from the 2013 BASIN survey. Deep-Sea Res. II. (submitted).

Eiane, K., Aksnes, D.L., Bagøien, E., Kaartvedt, S., 1999. Fish or jellies—a question of visibility? Limnol. Oceanogr. 44, 1352–1357.

Escobar-Flores, O'Driscoll, R., Montgomery, J., 2018. Spatial and temporal distribution patterns of acoustic backscatter in the New Zealand sector of the Southern Ocean. Mar. Ecol. Prog. Ser. 592, 19–35.

Fröb, F., Olsen, A., Våge, K., Moore, G.W.K., Yashayaev, I., Jeansson, E., Rajasakaren, B., 2016. Irminger Sea deep convection injects oxygen and anthropogenic carbon to the ocean interior. Nat. Commun. 7 https://doi.org/10.1038/ncomms13244, 13244.

Haraldsson, M., Tönnesson, K., Tiselius, P., Thingstad, T.F., Aksnes, D.L., 2012. Relationship between fish and jellyfish as a function of eutrophication and water clarity. Mar. Ecol.: Prog. Ser. 471, 73–85.

Harrison, W.G., Borsheim, K.Y., Li, W.K.W., Maillet, G.L., Pepin, P., Sakshaug, E., Skogen, M.D., Yeats, P.A., 2013. Phytoplankton production and growth regulation in the Subarctic North Atlantic: A comparative study of the Labrador Sea-Labrador/Newfoundland shelves and Barents/Norwegian/Greenland seas and shelves. Progress in Oceanography 114, 26–45.

Harrison, W.G., Li, W.K.W., 2007. Phytoplankton Growth and Regulation in the Labrador Sea: Light and Nutrient Limitation. J. Northw. Atl. Fish. Sci. 39, 71–82. https://doi.org/10.2960/J.v39.m592.

Holliday, N.P., Waniek, J.J., Davidson, R., Wilson, D., Brown, L., Sanders, R., Pollard, R. T., Allen, J.T., 2006. Large-scale physical controls on phytoplankton growth in the Irminger Sea Part I: Hydrographic zones, mixing and stratification. Journal of Marine Systems 59, 201–218.

Hudson, J.M., Steinberg, D.K., Sutton, T.T., Graves, J.E., Latour, R.J., 2014. Myctophid feeding ecology and carbon transport along the northern Mid-Atlantic Ridge. Deep-Sea Res. Part I 93, 104–116. https://doi.org/10.1016/j.dsr.2014.07.002.

Huse, G., Holst, J.C., Utne, K., Nøttestad, L., Melle, W., Slotte, A., Ottersen, G., Fenchel, T., Uiblein, F., 2012. Effects of interactions between fish populations on ecosystem dynamics in the Norwegian Sea – results of the INFERNO project. Mar. Biol. Res. 8, 415–419.

Irigoien, X., Klevjer, T.A., Røstad, A., Martinez, U., Boyra, G., Acuña, J.L., Bode, A., Echevarria, F., Gonzalez-Gordillo, J.I., Hernandez-Leon, S., Agusti, S., Aksnes, D.L., Duarte, C.M., Kaartvedt, S., 2014. Large mesopelagic fishes biomass and trophic efficiency in the open ocean. Nat. Commun. 5, 3271.

Kaartvedt, S., 2008. Photoperiod may constrain the effect of global warming in arctic marine systems. J. Plankton Res. 30, 1203–1206. https://doi.org/10.1093/plankt/fbn075.

Kiørboe, T., 2013. Zooplankton body composition. Limnol. Oceanogr. 58, 1843–1850. https://doi.org/10.4319/lo.2013.58.5.1843. https://search.crossref.org/?q=Ki%C3%B8rboe%2C+T.%2C+2013.+Zooplankton+body+composition.+Limnol.+Oceanogr.+58%2C+1843%E2%80%931850.

Klevjer, T.A., Kaartvedt, S., Bamstedt, U., 2009. In situ behaviour and acoustic properties of the deep living jellyfish *Periphylla periphylla*. J. Plankton Res. 31, 793–803. https://doi.org/10.1093/plankt/fbp036.

Klevjer, T.A., Torres, D.J., Kaartvedt, S., 2012. Distribution and diel vertical movements of mesopelagic scattering layers in the Red Sea. Mar. Biol. 159, 1833–1841.

Klevjer, T.A., Irigoien, X., Røstad, A., Fraile-Nuez, E., Benítez-Barrios, V.M., Kaartvedt, S., 2016. Large scale patterns in vertical distribution and behaviour of mesopelagic scattering layers. Sci. Rep. 6, 19873.

Klevjer, T., Melle, W., Knutsen, T., Strand, E., Korneliussen, R., Dupont, N., Salvanes, A. G.V., Wiebe, P.H., 2020a. Micronekton biomass distribution, improved estimates across four North Atlantic basins. Deep-Sea Res. Part II (this issue).

Klevjer, T.A., Melle, W., Knutsen, T., Aksnes, D.L., 2020b. Vertical distribution and migration of mesopelagic scatterers in four North Atlantic basins. Deep-Sea Res. Part II this issue.

Martin, E.S., Harris, R.P., Irigoien, X., 2006. Latitudinal variation in plankton size spectra in the Atlantic Ocean. Deep-Sea Res. Part II 53, 1560–1572. https://doi.org/10.1016/j.dsr2.2006.05.006.

Melle, W., Thor Klevjer, Espen Strand, Peter Wiebe, Aril Slotte, Geir Huse. (This issue). Fine-scale observations of physical and biological environment along a herring feeding migration route. This issue.

Naustvoll, L-J, Webjørn Melle, Thor Klevjer, Kenneth F. Drinkwater, Espen Strand, Tor Knutsen (this issue). Dynamics of primary production and species composition of phytoplankton in the North Atlantic during spring and summer - a trans-Atlantic survey. This issue.

Norheim, E., Klevjer, T., Aksnes, D., 2016. Evidence for light-controlled migration amplitude of a sound scattering layer in the Norwegian Sea. Mar. Ecol. Prog. Ser. 551, 45–52. https://doi.org/10.3354/meps11731.

Ohman, M.D., Frost, B.W., Cohen, E.B., 1983. Reverse diel vertical migration: an escape from invertebrate predators. Science 220, 1404–1407. https://doi.org/10.1126/science.220.4604.1404. https://search.crossref.org/?q=Ohman%2C+M.D.%2C+Frost%2C+B.W.%2C+Cohen%2C+E.B.%2C+1983.+Reverse+diel+vertical+migration%3A+an+escape+from+invertebrate+predators.+Science+220%2C+1404%E2%80%931407.

Palsson, O.K., Gislason, A., Gudfinnsson, H.G., Gunnarsson, B., Olafsdottir, S.R., Petursdottir, H., Sveinbjornsson, S., Thorisson, K., Valdimarsson, H., 2012. Ecosystem structure in the Iceland Sea and recent changes to the capelin (*Mallotus villosus*) population. ICES J. Mar. Sci. 69, 1242–1254.

Prokopchuk, I., Sentyabov, E., 2006. Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to *Calanus finmarchicus* distribution and temperature conditions. ICES J. Mar. Sci. 63, 117–127.

Purcell, J., Arai, M., 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451, 27–44.

Purcell, J., Uye, S., Lo, W., 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Mar. Ecol. Prog. Ser. 350, 153–174. https://doi.org/10.3354/meps07093. https://search.crossref.org/?q=Purcell%2C+J.%2C+Uye%2C+S.%2C+Lo%2C+W.%2C+2007.+Anthropogenic+causes+of+jellyfish+blooms+and+their+direct+consequences+for+humans%3A+a+review.+Mar.+Ecol.+Prog.+Ser.+350%2C+153%E2%80%93174.

Rey, F., 2004. Phytoplankton: the Grass of the Sea. In: Skjoldal, H.R., Sætre, R., Færno, A., Misund, O.A., h, I. (Eds.), The Norwegian Sea Ecosystem. Tapir Academic Press, Trondheim, Norway, pp. 97–136.

Sanders, R., Brown, L., Henson, S., Lucas, M., 2005. New production in the irminger basin during 2002. J. Mar. Syst. 55, 291–310.

Schnedler-Meyer, N.A., Mariani, P., Kjørboe, T., 2016. The global susceptibility of coastal forage fish to competition by large jellyfish. Proc. R. Soc. B. 28320161931 https://doi.org/10.1098/rspb.2016.1931.

Skjoldal, H.R. (Ed.), 2004. The Norwegian Sea Ecosystem. Tapir Academic Press, Trondheim, p. 559.

Skogen, M.D., Budgell, W.P., Rey, F., 2007. Interannual variability in Nordic seas primary production. ICES J. Mar. Sci. 64, 889–898.

Stenevik, E.K., Melle, W., Gaard, E., Gislason, A., Broms, C.T.A., Prokopchuk, I., Ellertsen, B., 2007. Egg production of *Calanus finmarchicus* - a basin-scale study. Deep-Sea Res. Part II 54, 2672–2685.

Strand, E., Klevjer, T., Knutsen, T., Melle, W., Ecology of mesozooplankton across four North Atlantic basins. Deep-Sea Res. Part II. (this issue).

Sverdrup, H.U., 1953. On conditions for the vernal blooming of phytoplankton. J. Conseil Int. Explor. Mer. 18 (3), 287–295.

Turner, J.T., 2015. Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump. Prog. Oceanogr. 130, 205–248. https://doi.org/10.1016/j.pocean.2014.08.005.

Våge, K., Pickart, R.S., Sarafanov, A., Knutsen, Ø., Mercier, H., Lherminier, P., Van Aken, H.M., Meincke, J., Quadfasel, D., Bacon, S., 2011. The Irminger Gyre: circulation, convection, and interannual variability. Deep-Sea Res. I 58 (5), 590–614.

Varpe, Ø., Fiksen, Ø., 2010. Seasonal plankton–fish interactions: light regime, prey phenology, and herring foraging. Ecol. 91, 311–318. https://doi.org/10.1890/08-1817.1. https://search.crossref.org/?q=Varpe%2C+%C3%98.%2C+Fiksen%2C+%C3%98.+2010.+Seasonal+plankton%E2%80%93fish+interactions%3A+light+regime%2C+prey+phenology%2C+and+herring+foraging.+Ecol..+91%2C+311%E2%80%93318.

Waniek, J.J., Holliday, N.P., 2006. Large-scale physical controls on phytoplankton growth in the Irminger Sea, Part II: Model study of the physical and meteorological preconditioning. Journal of Marine Systems 59, 219–237.

Wiebe, P.H., 1988. Functional regression equations for zooplankton displacement volume, wet weight, dry weight, and carbon: a correction. Fish. Bull. 86, 833–835.

Yashayaev, I., Loder, J.W., 2016. Recurrent replenishment of Labrador Sea Water and associated decadal-scale variability. J. Geophys. Res. Oceans 21, 8095–8114.